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ENVIRONMENTAL EFFECTS ON ROOSTING BEHAVIOR OF CHIMNEY SWIFTS

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The Chimney Swift (*Chaetura pelagica*) is widespread and abundant in eastern North America. The lengthy migration and long-unknown wintering grounds of this species early attracted attention, but detailed ecological research on this species began only in the middle of this century (Fischer 1958). Others have focused on responses by swifts to environmental conditions. Ramsey (1970), for example, studied the effect of changing ambient temperatures upon internal body temperatures, and Michael and Chao (1973) showed associations between roosting behavior, time of sunset and light intensity. Here we relate roosting and other behaviors to several environmental variables.

STUDY AREA AND METHODS

Our studies were conducted in Macomb, McDonough Co., Illinois. Midsummer daily temperatures range from 18–36°C. The center of the city has several blocks of contiguous 3- to 5-story buildings; the central area is surrounded on each side by about 10 blocks of 1- to 3-story homes averaging 10 m apart. Because Macomb is surrounded by cultivated farmland and is the largest city (population 23,000) in a 60 km radius, it holds the major portion of the Chimney Swift population in the area.

The first Chimney Swifts usually arrive in mid-April. Numbers are low until late April and early May, when the first large flocks are seen. The city contains a large population of swifts (1000–3000) until nest-building begins in late May, when numbers decline to fewer than 1000. During June and July, most chimneys with swifts contain 1 breeding pair with occasional visitors or nest helpers (see Dexter 1952, 1974). A few chimneys contain flocks consisting of non-breeding swifts (up to 300) or both a nesting pair and a flock (Zammuto and Franks 1978). Nesting occurs throughout the city from early June to August. Population numbers peak during September and slowly decrease until mid-October when all the swifts are gone for the winter.

Roosts of 6 or more individuals were analyzed. We located most roost-sites from a car at dusk by watching for circling flocks of swifts. Individual roost-sites were studied for several mornings and/or evenings. Those sites used most by swifts were observed most often.

A photometer placed on top of a car roof facing the open sky was used to measure light intensity. For each foot-candle (fc) change in light intensity during exit or entrance by swifts, the time and number of birds (tallied on hand counter) that left or entered a chimney were recorded. These data were tested using exponential curvilinear correlation and regression analyses.

The times when the majority of swifts left or entered a roost-site were determined with a stopwatch and an average time, designated as the time of peak exit or entrance, was computed. Temperatures and wind velocities were measured 1.5 m above ground near each roost-site. Cloud cover was estimated to the nearest 5%. These measurements and the times of sunrise and sunset were examined in relation to the time of peak exit and entrance at the roost-site using multiple regression and correlation analyses. The mean difference between time of

peak exit and time of sunrise and between time of peak entrance and time of sunset were analysed with regard to sky haziness and precipitation using *t*-tests. Sky haziness indicated that a fair sky was somewhat hazy, not clear blue. Precipitation was recorded as present or absent. Throughout this report, means appear with ±1 SD unless otherwise indicated.

RESULTS AND DISCUSSION

The mean number of Chimney Swifts recorded leaving a roost-site (N = 32) was 70 on 203 mornings, and the mean number entering was 83 on 166 evenings. A total of 224 flock departures or entries was observed at the 32 different chimneys. Of the 224, 65% of the departures or entries were of less than 100 individuals (Fig. 1).

Behavior at departure.—The swifts could usually be heard calling inside the chimney when we arrived at the roost 0.5 h before daylight. The calling became louder as daylight approached (about 0.2 fc), and continued during exit by swifts.

On many mornings, 1–10 swifts arrived at a roost-site about 20 min before any swifts left. Sometimes they circled the chimney and then flew away but more often they entered the chimney. The roosting birds called more loudly if any of these swifts entered the chimney, but the calling subsided after about 15 sec.

Swifts departed roost-sites singly or in small groups, almost always in a steady flow at rates of 4–150 per min. Sometimes a 30-min interval occurred between departure of 2 substantial portions of a flock.

Morning returns to roost-site.—After swifts left a chimney, some birds reentered on about 50% of the mornings. About 18% of 14,144 departing birds reentered within 30 min after first departure, and 3% reentered between 30 and 60 min. On about 3% of the mornings, more swifts entered a chimney than had left it only minutes before.

Swifts often circled the chimney without reentering for many minutes. When 1 circling swift entered, many other circling birds immediately followed in quick succession; the rest circled without reentering for several more minutes until another bird entered, followed by another portion of the group.

Weather conditions seemed to affect reentry into the roost. On cold or rainy mornings, over 90% of the swifts that left a chimney reentered it within 30 min. On these mornings, some were reentering while others were leaving. A shortage of insects in the air may also cause reentry. The number of insects in flight was likely very high at daybreak but probably declined sharply after sunrise (McClure 1938; Glick 1939, 1957). Reduced aerial prey may have caused the swifts to reenter the roost-site at sunrise (on the average of 11 min after departure) where they remained until later in the morning.

Evening observations of behavior.—Entry into the roost in the evening

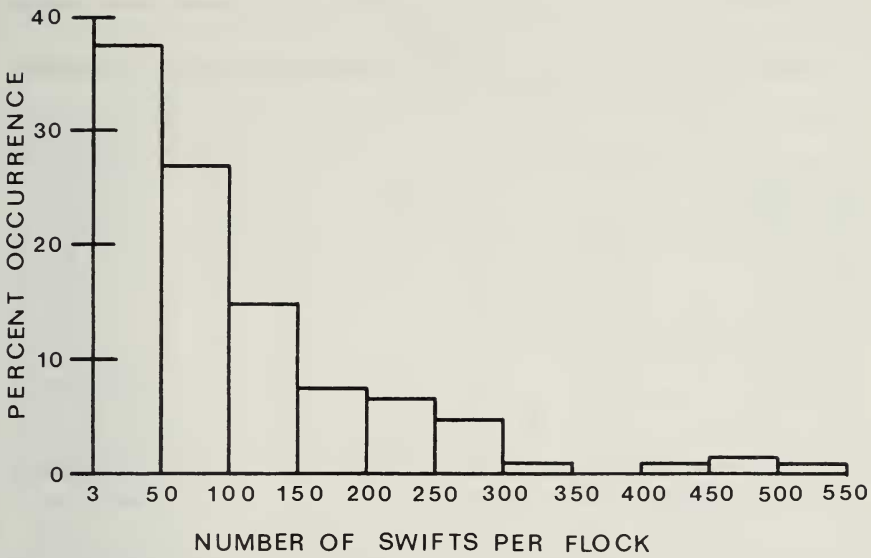

FIG. 1. Size of 224 flocks.

is described in detail by various authors (James 1950, Zammuto 1978). Often more than 50 swifts per min entered the chimney if light levels dropped to 0.5 fc with most of the flock still outside. Reentry rate in the morning was usually lower, so we believe approaching darkness is a major stimulus for entering the roost at dusk. However, as reported by Calhoun (1938), there were many evenings when only a few swifts were seen at any one time near a roost-site. As soon as they entered, additional small groups moved into the area and entered the chimney until the whole flock was inside.

Alterations in roosting behavior.—Various human-related activity disrupted swift roosting patterns. Fumes from furnaces, noises from loud vehicles, slamming doors and voices sometimes caused the swifts to leave the roost early, or caused circling swifts to disperse from the roost-site. On 60% of the summer evenings loudly calling swifts flying near roost-sites seemingly caused all the swifts in the area to disperse, although most usually returned within 3 min.

On nearly 50% of the evenings, late-arriving individual swifts circled the roost a few times but then flew off (Coffey 1936). Koskimies (1950) felt that such behavior in the Common Swift (*Apus apus*) indicated it was too dark for the swifts to see well enough to enter the roost, and thus swifts overtaken by nightfall spent the night on the wing.

TABLE 1

MONTHLY MEAN LIGHT INTENSITY (FOOT-CANDLES) WHEN THE SWIFTS ENTERED THE ROOST

Date	No. swifts	No. evenings observed	Mean ± SE	Light intensity mode
Sept. 1976	207	3	0.6 ± 0.35	0.5
Oct. 1976	623	8	0.7 ± 0.17	0.5
April 1977	401	4	0.5 ± 0.28	0.5
May 1977	1937	18	1.8 ± 0.30	0.5
June 1977	2853	25	2.7 ± 0.23	0.5
July 1977	2474	14	3.3 ± 0.33	0.5
Aug. 1977	886	10	3.5 ± 0.44	1.5
Sept. 1977	1934	19	1.0 ± 0.14	0.5
Oct. 1977	183	2	1.1 ± 0.37	0.5
Total	11,498	103	overall $\bar{x}$ = 1.7 ± 1.2[a]	0.6

[a] Standard deviation of the 9 monthly means shown.

Light intensity.—Morning departure of the swifts was more widely distributed at very low light intensities than was evening descent. Based on 12,430 birds, 70% left the chimney during light of 0 and 7 fc, while a similar percentage of 11,498 birds entered between a more restrictive 0 and 2 fc.

Light intensity was negatively correlated with the number of swifts leaving the roost each morning ($r = -0.87$, $P < 0.001$) and entering the roost each evening ($r = -0.63$, $P < 0.001$). The regression formula for the

TABLE 2

MONTHLY MEAN LIGHT INTENSITY (FOOT-CANDLES) WHEN THE SWIFTS LEFT THE ROOST

Date	No. swifts	No. mornings observed	Mean ± SE	Light intensity mode
Oct. 1976	634	11	6.7 ± 0.62	0.5
April 1977	391	3	8.0 ± 1.56	2.5
May 1977	1668	16	2.3 ± 0.21	1.5
June 1977	2104	25	3.7 ± 0.24	2.5
July 1977	2982	17	7.0 ± 0.46	2.5
Aug. 1977	1900	13	4.1 ± 0.49	3.5
Sept. 1977	2185	16	8.1 ± 0.44	7.5
Oct. 1977	394	4	4.4 ± 0.57	2.5
Total	12,430	105	overall $\bar{x}$ = 5.5 ± 2.2[a]	2.9

[a] Standard deviation of the 8 monthly means shown.

TABLE 3

EQUATIONS AND CORRELATIONS SHOWING THE EFFECT OF ENVIRONMENTAL VARIABLES ON THE MEAN TIME OF PEAK EXIT AND ENTRANCE AT THE ROOST-SITE

	Exit			Entrance		
Independent variable	Equation[a]	Coefficient of determination[b]	No. mornings	Equation[a]	Coefficient of determination[b]	No. evenings
Time of sunrise	$Y = -0.37 + 1.0X$	0.96***	114			
Time of sunset				$Y = 0.40 + 1.0X$	0.98***	114
Temperature (°C)	$Y = 7.1 - 0.072X$	0.43***	114	$Y = 18.2 + 0.092X$	0.32***	114
Wind speed (km/h)	$Y = 6.1 - 0.044X$	0.05*	113	$Y = 20.1 + 0.06X$	0.05**	114
Percent cloud cover	$Y = 6.0 - 0.002X$	0.02	109	$Y = 20.2 + 0.002X$	0.01	112

[a] Where Y is the mean time (24-h clock, CDT) of peak exit from or entrance into the roost-site and where X is the independent variable listed.

[b] Levels of significance as determined by F tests: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

number of swifts (Y) leaving and entering the roost with respect to each level of light intensity (fc) was $Y = 17.3e^{-0.050^{fc}}$ at dawn and $Y = 13.1e^{-0.131^{fc}}$ in the evening.

The swifts entered the roost at significantly higher light intensities in the warmer months (May through August) than in the colder months (April, September, October) ($t = 5.68$, df = 7, $P < 0.001$) (Table 1). In a Texas study by Michael and Chao (1973), May through August was also when swifts entered the roost at higher mean light intensities, although in their study, light intensities at entrance were much higher (ranging between 2.0 and 14.2 fc, $\bar{x} = 5.9 \pm 3.7$) than the ones we observed (0.5–3.5 fc, $\bar{x} = 2.0 \pm 1.1$; for 1977, Table 1). Mean monthly light intensities at which swifts left roost-sites are shown in Table 2.

Sunrise and sunset.—The times of sunrise and sunset were more closely associated with the mean time of peak exit or entrance at the roost than temperature, wind speed, or cloudiness (Table 3).

Swifts left the roost about 11 min before sunrise and entered it about 21 min after sunset (Table 4). There was less than a 10 min difference among monthly means. In spring and summer in Texas, swifts entered the roost much sooner after sunset ($\bar{x} = 14 \pm 2$ min, range 12–16 min) (Michael and Chao 1973) than did swifts in our study for all months.

Temperatures.—Swifts left the roost significantly later and entered it

TABLE 4

TIMES BEFORE SUNRISE AND AFTER SUNSET WHEN SWIFTS LEFT AND ENTERED THE ROOST-SITE AT THE FASTEST RATE

Date	No. mornings	Monthly mean minutes before sunrise ± SE	No. evenings	Monthly mean minutes after sunset ± SE
Sept. 1976	11	9.8 ± 1.8	11	22.4 ± 1.3
Oct. 1976	11	11.7 ± 1.7	7	22.6 ± 1.7
April 1977	3	7.7 ± 2.9	4	21.8 ± 0.8
May 1977	15	17.3 ± 0.9	18	23.1 ± 1.3
June 1977	24	12.2 ± 1.7	27	21.9 ± 1.2
July 1977	17	10.7 ± 0.9	15	18.0 ± 2.1
Aug. 1977	13	12.3 ± 2.7	13	17.1 ± 0.8
Sept. 1977	16	9.0 ± 1.2	18	18.6 ± 0.7
Oct. 1977	4	8.9 ± 1.9		
Total	114	overall $\bar{x}$ = 11.1 ± 2.8[a]	total 113	overall $\bar{x}$ = 20.7 ± 2.4[b]

[a] Standard deviation of the 9 monthly means shown.
[b] Standard deviation of the 8 monthly means shown.

significantly earlier on colder days (Table 3). Koskimies (1950) found that *A. apus* did not leave the roost-site until the air temperature was high enough for normal numbers of flying insects to be available. Chimney Swifts may behave similarly. In southern Texas, Glick (1939, 1957) found that the greatest numbers of insects were in the air at 25°C, and that numbers of insects decreased considerably below 18°C; very few were flying at temperatures below 15.6°C.

Wind speed, cloud cover and haziness.—With higher wind speeds, the swifts leave the roost earlier in the morning and stay out later in the evening (Table 3). Numbers of flying insects may be an important factor; Glick (1939, 1957) found that the abundance of insects in flight decreased as winds dropped below 8 km/h. Therefore, fewer insects were flying and presumably less food was available for swifts on calmer days. It may be more advantageous to be roosting when the food supply reaches some lower threshold. Neither cloud cover (Table 3) nor sky haziness had significant ($P > 0.05$) effects on the time of peak exit or entrance.

Precipitation.—Rainfall significantly delayed the time of peak exit from the roost (mean exit time on 10 rainy mornings = 0.3 min before sunrise, mean on 103 fair mornings = 12.5 min before sunrise, $P < 0.001$). On rainy mornings, the swifts usually stayed in the chimney until the rain stopped, but if they did depart in the rain, most quickly reentered. In sporadic rain, the reentry corresponded to the periods of rain. Rainy weather also delayed the onset of daily activity in *A. apus* (Koskimies 1950), probably due to a reduction of the food supply. If the rain continued for several consecutive

days, the Chimney Swifts did not return to the roost in the morning after the first 2 days. They were probably forced to hunt in the poor weather to keep from starving, or moved elsewhere.

On 5 days, Chimney Swifts circled roost-sites when summer afternoon thunderstorms threatened. During most storm threats, Chimney Swifts flew low, resuming their normal clear day flying height when the threat passed as observed for Black Swifts (*Cypseloides niger*) (Rathbun 1925). Between intermittent rain showers, the swifts we were studying usually flew in small flocks, flying lower than usual. They may have been following their food supply; Koskimies (1950) found that many insects were washed down to the ground by rain. Some swifts in our study were repeatedly observed flying close to lawns when it rained (Zammuto and Franks 1979). *A. apus* reduced foraging activity in rain (Koskimies 1950, Lack and Lack 1951).

When it rained, Chimney Swifts entered the roost-site earlier (mean of 8 rainy evenings = 16.3 min after sunset, mean of 104 fair evenings = 20.9 min after sunset, $P < 0.05$). On most rainy evenings about 10% of any flock entered the roost 30 min before the rest of the birds. If the rain stopped after such early entrances some birds left the roost.

James (1950), Bowman (1952) and Fischer (1958) noticed increases, but Dexter (1966, 1968) noticed decreases in roosting flock sizes during prolonged, cool, rainy periods. In our study, swift numbers increased at 10 roost-sites during 10 such periods. Some flock sizes doubled, reaching 200 or more birds. Since in the summer months these added birds in our study were probably not migrants (Zammuto 1978), we postulate that they moved from smaller roosts. Presumably, loss of body heat would be minimized when many swifts formed tight roosting clusters than when only a few swifts were present. This would allow the swifts to survive longer without food since they stayed in the roost-site during cool, rainy weather. Dexter (1966) noted that flocks he observed decreased in numbers in inclement weather and he hypothesized that absent birds were roosting in warmer chimneys elsewhere. Our experience suggests that they were in a larger roost, but we never studied small roosts during rainy periods to see if swift numbers decreased.

SUMMARY

Roosting of Chimney Swifts was studied in relation to several environmental variables in September and October 1976 and April through October 1977. An average of 70 swifts were recorded leaving and 83 entering 32 different roost-sites on 203 mornings and 166 evenings. Of 224 flocks, 65% numbered below 100 individuals. About 18% of the swifts that left the roost-site at dawn returned to it to reenter around sunrise. In the morning, 70% of the swifts left the chimney during light intensities of 0–7 fc, but in the evenings 70% entered between a more restrictive 0 and 2 fc. Swifts left the roost-site at 5.5 ± 2.2 fc, 11.1 ± 2.8 min before sunrise and entered at 1.7 ± 1.2 fc, 20.7 ± 2.4 min after sunset. Light intensity, time of

sunrise and sunset, temperature, wind speed and precipitation were all associated with the time of departure from and entrance into the roost-site. Swifts left the roost-site later and entered it earlier on colder days, on days with precipitation, and on calmer days. The effect of sky haziness and cloud cover upon time of peak exit and entrance was not significant. All the environmental variables reported to affect flying insect abundance were similarly associated with swift activity patterns.

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